



Volatiles as inducers and suppressors of plant defense and immunity — origins, specificity, perception and signaling

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Volatiles from attacked plants, microbes and herbivores can enhance plant defenses. However, the absence of volatiles rather than their presence has sometimes been associated with enhanced defense, suggesting that volatiles may also act as defense suppressors. Recent work provides a potential mechanistic explanation for these observations by showing that volatile cues can modulate different hormonal pathways, including jasmonate (JA), salicylic acid (SA) and auxin (IAA) signaling. Many of these pathways interact with each other through crosstalk. Thus, volatiles may suppress plant defenses through negative hormonal crosstalk. Hormonal crosstalk may also allow plants to integrate different volatile cues to respond specifically and appropriately to environmental change.

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Introduction

The capacity to perceive and respond to environmental cues is essential to all life on earth. Volatile molecules can deliver information about the presence, abundance and status of a given volatile emitter in the form of airborne cues. Plants for instance respond to volatile cues from various origins, including plants, microbes and herbivores [1–5]. Environmental volatiles (*i.e.* volatiles that emanate from other tissues or sources and reach a given plant part through headspace diffusion) may act both as positive or negative regulators of plant defenses [6,7,8*,9*,10*]. While the mechanisms underlying positive defense regulation have been partially elucidated [10*,11], if and how volatiles suppress plant defenses is less clear. Several recent studies demonstrate that environmental volatiles

can activate different hormonal signaling cascades [12*,13*,14], some of which are connected through cross-talk. These findings open up the possibility that volatiles may modulate hormonal networks and change defenses both positively and negatively. Here, I discuss how hormonal crosstalk may mediate specificity and integration of different environmental volatile cues into plant defense responses. I argue that merging plant volatile and phytohormone research has the potential to increase our understanding of how plants translate volatile cues into specific and appropriate defense responses.

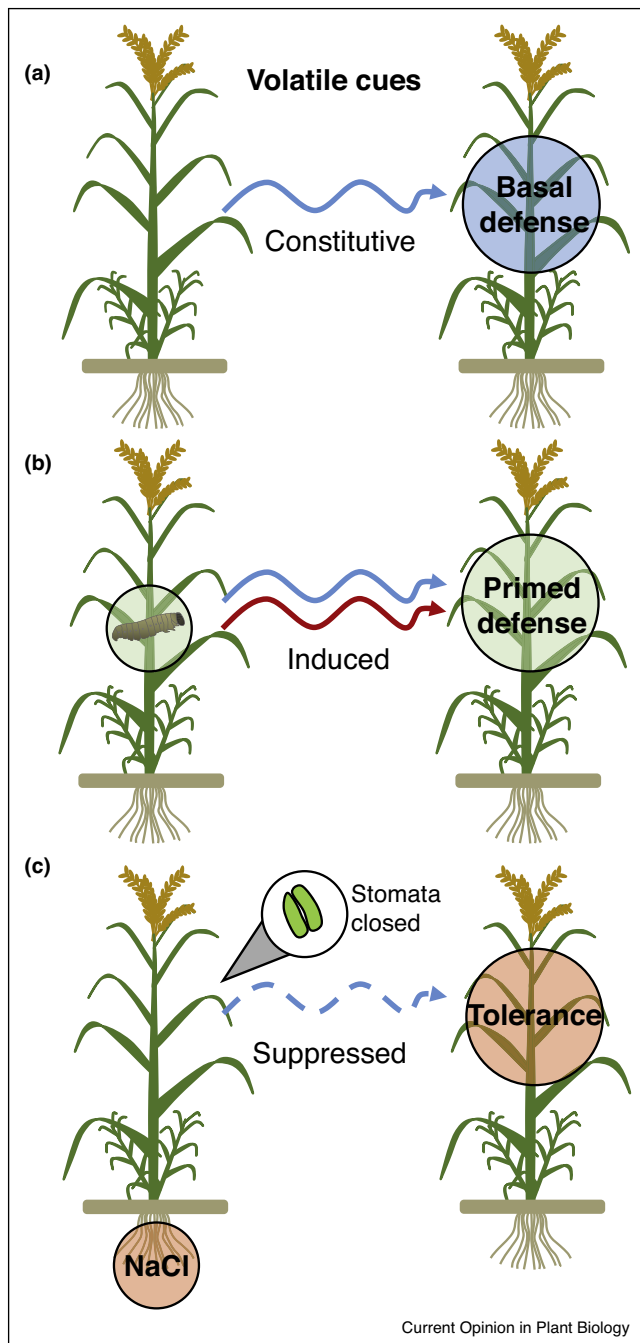
Many stress-related volatiles enhance plant defense

In many cases, environmental volatiles have been found to act as positive regulators of plant defenses. A variety of stress-induced plant volatiles for instance can prime or induce plant defense responses (Figure 1a,b). The growing list includes herbivore-induced and pathogen-induced green leaf volatile (GLV) alcohols, esters and aldehydes, terpenes and aromatic compounds [14,15,13*]. Volatile cues from other kingdoms of life can also trigger plant defense responses. Various bacterial and fungal volatiles can increase plant pathogen resistance *in vitro* and *in vivo* [5,16,10*]. Furthermore, the herbivore-derived volatile (*E,S*)-conophthorin has recently been documented to induce defensive signaling [9*]. How environmental volatiles are perceived and activate defense signaling remains unknown, but several potential mechanisms may be at play (Box 1).

The absence of volatiles can enhance plant defenses — a case for volatile suppressors?

Although stress-related volatile cues are often acting as positive regulators of plant defense, experiments in *Nicotiana attenuata* demonstrated that the absence rather than the presence of GLVs from volatile blends of herbivore-attacked plants is associated with the induction of defense-related genes [6]. The prevalence and biological significance of these volatile ‘sounds of silence’ [24] has long remained unclear. A recent study documented that broad bean plants can respond to airborne cues from salt-stressed neighbors by increasing their salinity tolerance [8*] (Figure 1c). This response was associated with a suppression rather than an induction of volatile emissions from the stressed neighbors [8*]. As salt stress leads to stomatal closure, it is perhaps no surprise that volatile emissions decreased in the emitter plants. Stomatal

Figure 1



Presence or absence of volatiles can indicate stress in a neighboring plant. Plants emit a bouquet of constitutive volatiles (a). Upon pathogen or herbivore-attack, plants emit additional volatiles which can prime or induce defense responses in neighboring plants (b). Abiotic stress such as salt or drought stress can lead to stomatal closure and may thereby reduce constitutive volatile emissions, which may also activate stress tolerance mechanisms (c). While (a) and (b) are well established, the prevalence and importance of (c) is less clear. For references and specific examples, see main text.

Box 1 Mechanisms of volatile perception and integration.

Environmental volatiles may be integrated into plant defenses through several mechanisms. Examples for each mechanism are given below.

Volatiles may act as hormonal precursors. Methyl jasmonate (MeJA) and methyl salicylate (MeSA) can be converted to phytohormones by demethylation and can thereby induce defense signaling pathways [17]. Indole may act as a precursor of the auxin indole-3-acetic acid (IAA) [18].

Volatiles may be taken up and converted to toxins. The GLV (Z)-3-hexen-1-ol can be absorbed and converted to (Z)-3-hexenyl vicinonide, which reduces herbivore growth [19].

Volatiles may dissolve into membranes. Indole can diffuse through bacterial membranes and can act as an ionophore that decreases membrane potentials at concentrations above 3 mM [20]. GLVs and lipophilic volatiles have also been proposed to change membrane potentials by dissolving into membranes [21].

Volatiles may bind to receptor proteins. Endogenous ethylene can bind to five structurally and functionally different receptor proteins in Arabidopsis [22].

In most cases, the involvement of these mechanisms in the perception and integration of environmental volatiles in plants is not well understood. Furthermore, how volatiles reach cell membranes and/or the cell interior is unclear. Recent work has identified volatile transporters that transfer volatiles across the plasma membrane [23*]. It is thus conceivable that plant cells may be able to facilitate the import of volatiles from the environment.

closure is also elicited by various other stress conditions such as leaf damage, pathogen attack and drought and has been shown to reduce volatile emissions in maize [25]. Thus, it is conceivable that a reduction of constitutive volatile emissions may be indicative of a stressed neighbor.

From a mechanistic perspective, induction of defense in the absence of volatiles is likely the result of de-repression, where a volatile suppresses a defense response, and its absence then relieves this suppression and activates the defense. However, little is known about the capacity of volatiles to suppress plant defenses. GLV complementation in *N. attenuata* suppresses the induction of defense-related transcripts [6]. Furthermore, exposure of volatiles from damaged neighbors increases herbivore damage on blow-wives (*Achyraea mollis*) and leaf removal by a chewing herbivore on charlock (*Sinapis arvensis*) [7], pointing to a suppression of resistance by wound-induced volatiles. Clearly, more work is required to understand the identity and prevalence of plant-defense suppressing volatiles.

Volatile cues can elicit different signaling cascades involved in plant defense and innate immune responses

One possibility by which volatiles may act as negative regulators of plant defenses is negative hormonal cross-talk [26]. To evaluate this hypothesis, we first need to

understand which signaling pathways can be activated by volatile cues. Many volatiles increase plant defense by enhancing JA signaling. Early work demonstrated that green-leaf volatiles (GLVs) that are emitted by wounded leaves transiently induce and prime jasmonates (JA) in non-wounded maize leaves [27], resulting in a stronger induction of JA-dependent defenses upon subsequent herbivore attack [28]. GLVs also activate and prime the expression of putative JA biosynthesis genes in lima bean and poplar [29,30] and enhance JA-induced responses in *Arabidopsis* [31]. Indole emitted by herbivore-attacked plants as well as (*E,S*)-conophthorin emitted by goldenrod gall fly (*Eurosta solidaginis*) males also prime JA production and downstream responses [9,32]. Furthermore, volatiles from *Trichoderma* fungi prime JA-responsive marker genes and defenses in *Arabidopsis* [10^{*}].

Recent work demonstrates that environmental volatiles can also act via other signaling pathways. In *Arabidopsis thaliana*, the GLV (*E*)-2-hexenal increases the expression of two WRKY transcription factors that are involved in GLV-induced root growth inhibition [33]. The same WRKYs also regulate γ -amino butyric acid (GABA) biosynthesis, which again mediates GLV-induced root growth inhibition in a JA-independent manner [34]. An oxidoreductase was recently found to regulate GLV-induced changes in mitochondrial redox status [12^{*}]. Based on these studies, it was suggested that GLVs may increase mitochondrial ROS by regulating GABA [12^{*}]. A recent study confirmed that environmental volatiles can influence ROS homeostasis; a mixture of α -pinene and β -pinene increases the accumulation of superoxide anion radicals in *Arabidopsis* leaves more than 2-fold [13^{*}].

In *Arabidopsis*, monoterpenes not only increase ROS, but also promote systemic acquired resistance (SAR) through salicylic acid (SA) and azelaic acid (AzA) signaling [13^{*}]. Increased expression of a homologue of the SA marker gene PR-2 was also observed in lima bean plants exposed to volatiles from benzothiadiazole (BTH)-treated plants [35]. Furthermore, MeSA has been proposed as a volatile cue that can directly activate SA signaling and SAR [36], even though the importance of MeSA as an airborne volatile cue remains to be determined [37]. Overall, the recent literature shows that environmental volatiles can trigger the SA signaling pathway. SA signaling antagonizes JA signaling in many plant species [38], and environmental volatiles that induce SA signaling may therefore suppress JA-dependent defenses.

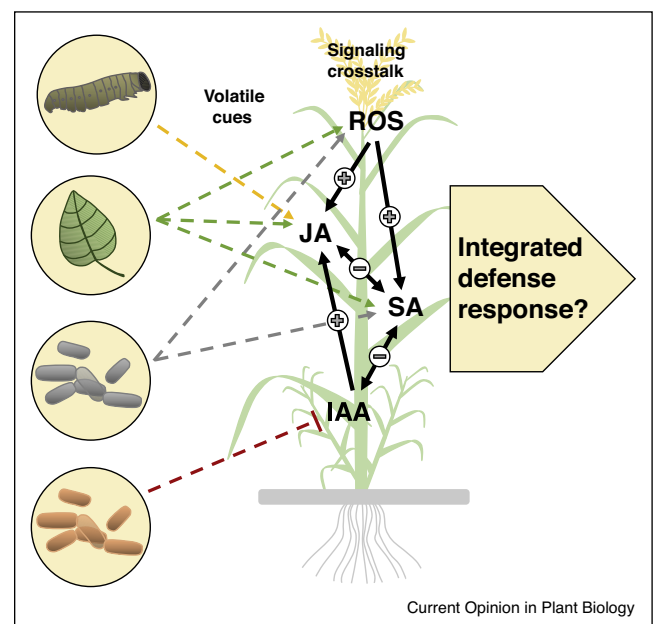
Advances in plant-microbe interactions have further expanded the repertoire of plant signaling pathways that can be modulated by volatile cues [5]. Indole, which is produced in high amounts by *Escherichia coli*, can inhibit TIR1-dependent auxin (IAA) signaling in *Arabidopsis*

roots in Petri dish experiments [39]. Whether indole has similar effects under natural conditions and doses remains to be investigated. IAA signaling potentiates JA signaling in *N. attenuata* [40]. Therefore, indole may indirectly suppress JA signaling by inhibiting IAA signaling. In maize however, indole enhances rather than suppresses JA signaling [34]. Targeted experiments will be required in the future to assess whether the impact of indole on IAA and JA signaling depends on the plant species, the exposed tissue, the exposure level or other factors.

Hormonal-cross talk and the integration of volatile cues

Volatiles can trigger different plant signaling cascades, which can interact with each other positively or negatively [40,26]. Thus, hormonal crosstalk provides a mechanism by which volatile cues can enhance or suppress plant defenses and innate immunity (Figure 2).

Figure 2



Signaling crosstalk may promote the integration of different volatile cues. Volatiles from plants, microbes and herbivores have been shown to affect different signaling cascades (left). Through crosstalk, volatiles may therefore act as defense activators or suppressors (center). Furthermore, different volatile cues may be integrated to yield unique defense responses (right). This may enable plants to prioritize defense responses or combine multiple volatiles from the same emitter into appropriate defense responses. While the effects of volatiles on different signaling molecules have been demonstrated, their integration through signaling crosstalk remains to be investigated. Straight lines: Interactions between signaling cascades. Dashed lines: Volatile cues from different sources. Expected positive crosstalk is indicated by a '+', while negative crosstalk is indicated by a '-'. For references and specific examples, see main text.

Box 2 Integration of multiple volatile cues by plants.

If and how plants integrate different volatile cues to increase the reliability of the obtained information is not well understood. Here, two examples are discussed to illustrate how different levels of integration may be required depending on the volatile source. First, Maize plants respond to herbivory-induced indole as well as the three GLVs (Z)-3-hexenal, (Z)-3-hexen-1-ol, and (Z)-3-hexenyl acetate by priming the jasmonate pathway [32,27]. GLVs are specific for plants, but relatively unspecific regarding herbivory [14], while indole is specifically released by leaves upon herbivore attack [42], but can also emanate from other plant tissues and organisms. Integrating the two cues may be advantageous for maize plants to obtain a more reliable signature for the presence of an attacking herbivore. Second, exposure to a single component of the goldenrod gall fly male pheromone blend, (*E,S*)-conophthorin, is sufficient to reduce larval damage to a similar extent than exposure to the full volatile blend [9]. Given that (*E,S*)-conophthorin is much less common in nature than typical herbivore-induced plant volatiles, it may be used as a relatively specific cue to detect male gall flies.

Hormonal crosstalk may also provide a means for plants to integrate different volatile cues. The ability to integrate several individual volatiles (*i.e.* to be able to use volatile blends) can help organisms to reliably detect a given condition when individual volatiles are redundant between different stressors and species [41]. The integration of multiple volatile cues may thus enable plants to more reliably detect the presence of a given environmental stressor and regulate the strength of their response according to the reliability of the detected volatile cues (Box 2). To date, suppression and integration of volatile cues by plants are not well studied, but advances in hormonal crosstalk provides a mechanistic framework to explore these important processes in the future [26]. Given the capacity of environmental volatiles to regulate different hormonal signaling cascades (Figure 2), one would expect that positive and negative interactions between volatile cues are frequent and widespread.

Conclusions

Plants respond to volatile cues from the environment by adjusting their defenses and innate immune responses. Our knowledge on volatile perception and integration is still rudimentary, but it is becoming clear that volatiles affect many different hormonal signaling cascades. This knowledge will help to predict the effects of volatiles on specifically regulated defenses through hormonal crosstalk in the future. Uncovering mechanistic links between volatile perception and hormonal signaling will be essential to understand how plants respond to volatile blends in natural and agricultural ecosystems.

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